

Four-bar linkage modeling in teleost pharyngeal jaws: computer simulations of bite kinetics

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Abstract:

The pharyngeal arches of the red drum (*Sciaenops ocellatus*) possess large toothplates and a complex musculoskeletal design for biting and crushing hard prey. The morphology of pharyngeal apparatus is described from dissections of six specimens, with a focus on the geometric conformation of contractile and rotational elements. Four major muscles operate the rotational 4th epibranchial (EB4) and 3rd pharyngobranchial (PB3) elements to create pharyngeal bite force, including the levator posterior (LP), levator externus 3/4 (LE), obliquus posterior (OP), and 3rd obliquus dorsalis (OD). A biomechanical model of upper pharyngeal jaw biting is developed using lever mechanics and four-bar linkage theory from mechanical engineering. A pharyngeal four-bar linkage is proposed that involves the posterior skull as the fixed link, the LP muscle as input link, the epibranchial bone as coupler link, and the toothed pharyngobranchial as output link. We used a computer model to simulate contraction of the four major muscles, with the LP as the dominant muscle whose length determined the position of the linkage. When modeling lever mechanics, we found that the effective mechanical advantages of the pharyngeal elements were low, resulting in little resultant bite force. In contrast, the force advantage of the four-bar linkage was relatively high, transmitting approximately 50% of the total muscle force to the bite between the toothplates. Pharyngeal linkage modeling enables quantitative functional morphometry of a key component of the fish feeding system, and the model is now available for ontogenetic and comparative analyses of fishes with pharyngeal linkage mechanisms.

Key Words: muscle contraction, feeding, fishes, morphometrics, levers, kinematic transmission

Introduction:

Capturing, crushing, and chewing prey in vertebrates conjures visual images of large carnivores like lions, crocodiles, and sharks gnashing powerful oral jaws filled with large pointed and sharp cutting teeth. For many bony fishes, these forceful acts of prey processing are hidden from view occurring among gills arch elements that have become secondarily modified into a feeding apparatus of versatile biting jaws. These pharyngeal jaws make up a highly complex functional system that can manipulate, winnow, macerate, transport, and crush prey items and have long been considered a major evolutionary innovation of euteleosts (Lauder, 1983b; Vandewalle et al., 2000). How pharyngeal jaws move and work has received limited attention due in part to their inaccessibility to visual recording techniques such as high-speed video. Cineradiography and sonomicrometry have however provided insights into the motions of the toothplates during pharyngeal transport behaviors in cyprinid and several perciform fishes (Lauder, 1983a; Liem and Sanderson, 1986; Sibbing, 1982). Wainwright (1989) proposed a mechanism of pharyngeal jaw biting in perciform fishes from functional morphology and electromyography experiments of prey processing in haemulid fishes. However, a biomechanical model of the bite kinetics and force generation of generalized perciform pharyngeal jaws remains an important next step in the exploration of pharyngeal jaw function and evolution.

Biomechanical models of feeding mechanisms in fishes have had considerable success over the years in emulating the dynamic motions of skull kinesis during prey capture (Westneat, 1990), revealing complex evolutionary patterns in morphological diversity and musculoskeletal function (Alfaro et al., 2004; Wainwright et al., 2004; Westneat, 2004), predicting variation in suction feeding performance among species (Carroll et al., 2004), and explaining

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ecomorphological patterns of prey use (Wainwright, 1987; Wainwright, 1995). Fish feeding models commonly utilize engineering principles of lever mechanics and four-bar linkage theory where the geometric transmission of force input from muscular contractions can be modeled across skeletal articulations and rotational joints to generate predictive metrics of jaw motions, speed, and force output of the feeding mechanism (Wainwright and Shaw, 1999; Westneat, 1990, 1991; Westneat, 1994). Recent advances in modeling the lower jaw closing mechanism in fishes have incorporated simulations of dynamic power output by employing Hill equation parameters for the non-linear force/velocity relationship of muscle shortening and have accounted for aquatic medium effects of inertia, pressure, and hydrodynamic drag (Wassenbergh et al., 2005; Westneat, 2003).

Prey processing among pharyngeal jaw elements is mediated through a network of branchial muscles that interact with each other, the neurocranium, pectoral girdle, and hyoid. Unlike the oral jaws of most bony fishes which are composed of generally eighteen to twenty bones and muscles, the branchial arches of pharyngognath fishes are much more complex. In the pharyngeal jaws alone, there are upwards of 43 muscles controlling the articulations among some 24 bones (Winterbottom, 1974). These elements together with interactions from peripheral systems such as the hyoid arch and pectoral girdle, can produce a myriad of joint articulations, rotational vectors, lever mechanics, and linkage motions. As a first step to understanding the biomechanical complexity of pharyngeal jaw kinetics, our study focuses on the upper jaw bite mechanism of generalized perciform fishes whereby the main upper pharyngeal toothplate performs a biting action by being ventrally depressed onto the prey as described by Wainwright (1989). It should be noted that our proposed model is not applicable for describing the biting actions of fishes that have a pharyngeal jaw apparatus that is modified as a muscular sling

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mechanism. The biomechanics and kinetics of the pharyngeal jaw muscular sling that is common in labrids, pomacentrids, embiotocids and cichlids where bite forces are directed dorsally from a mobile lower toothplate have already been examined in several labroid groups (Galis, 1992, 1997; Liem, 1973; Liem and Sanderson, 1986; Wainwright, 1987).

To mechanically model the biting action of the upper pharyngeal jaws, we chose the red drum (*Sciaenops ocellatus*, L.), a coastal sciaenid fish common in the southern United States and Gulf of Mexico, as possessing a musculoskeletal archetype for generalized perciform pharyngognathy. *Sciaenops ocellatus* attains large body size (i.e. 50 kg), and feeds on a range of prey, from hard-shelled crustaceans, such as crabs to softer bodied fishes and other more pliable marine invertebrates (Boothby and Avault, 1971; Overstreet and Heard, 1978; Scharf and Schlacht, 2000). Along with this varied diet, *S. ocellatus* has evolved robust pharyngeal jaws that are functionally versatile and adept at puncturing, cracking, shredding, and chewing engulfed prey making them excellent candidates for developing a pharyngognath model. However, while the ontogeny of bone and muscle masses of *S. ocellatus* pharyngeal jaws has been documented (Grubich, 2003), the functional morphology and biomechanics of the pharyngeal jaw mechanism in *S. ocellatus* has never been qualitatively or quantitatively described.

Using the branchial arches of *S. ocellatus* as a model functional system for prey processing in perciform fishes, the goals of this study are 1) to describe the functional morphology of the upper pharyngeal jaw mechanism in *S. ocellatus* 2) to present the first biomechanical model of pharyngeal biting based on lever mechanisms and four-bar linkage engineering theory 3) to develop a computer software program that can simulate jaw kinetics and predict dynamic force output of upper pharyngeal jaw bite performance in *S. ocellatus*.

Materials and Methods:

Specimen dissection

Six red drum (*Sciaenops ocellatus*) ranging in size from 533-660 mm TL were collected by hook and line in Florida coastal waters. After measurement, specimens were promptly labeled and frozen until dissection. Heads were thawed and the pharyngeal jaw anatomy was exposed through dissection of the parasagittal plane of the right side branchial arches. Dissections of the deep pharyngeal anatomy required the removal of the operculum, suspensorium, hyoid bar and oral jaws (Fig. 1). Gill filaments were then cut from the branchial arches and digital photos were taken during each stage of the dissection. Pharyngeal dissections removed the bones and associated musculature of the first two arches to reveal the main upper jaw biting elements of the 3rd and 4th branchial arches. Connective tissues covering the pharyngeal muscles and bones were then carefully removed to reveal the articulations of the musculoskeletal architecture of the upper jaw bite mechanism. To corroborate pharyngeal jaw dimensions estimated from digital photos by the computer model, muscle and bone lengths were measured with digital calipers. Muscle masses were also measured from the left side of each individual to be used in later models predicting force output of the pharyngeal bite (Table 1).

Digital photos of pharyngeal anatomy were taken with a 3.2 megapixel Sony Cybershot DSC-P5. Because the branchial arches are positioned at an oblique lateral angle to the main body axis of the fish (Fig. 2A) and four-bar linkages are by definition 2-dimensional planar mechanisms, photographs were taken of the pharyngeal anatomy *in situ* in a plane parallel to the 4th branchial arch. Images were then downloaded and musculoskeletal landmarks were digitized from the photographs with the custom image analysis software, tpsDig v.1.4 (Rohlf, 2004). In

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all, twelve landmarks were identified to represent a series of xy coordinates that define the component links of an upper pharyngeal jaw four-bar mechanism (Table 2, Fig. 3A).

Computer modeling of sciaenid pharyngeal jaws

The transmission of force and motion of the pharyngeal mechanism was modeled as a four-bar linkage, in a manner similar to previous dynamic linkage analyses of the opercular mechanism (Anker, 1974), hyoid mechanism (Muller, 1987a; Westneat, 1990) and oral jaws (Westneat, 1990; Westneat, 1994) of fishes. A computer model was developed as an application for the Apple Macintosh platform using Metrowerks CodeWarrior Pascal. The software, named PharyngoModel 2.0 (user interface shown in Fig. 4), is available free by internet download or directly from M. Westneat. The model accepts sets of Cartesian coordinates (Fig. 3) for multiple specimens that quantify the morphometrics of the pharyngeal mechanism. The first step of the model is to calculate a large set of initial distances and angles among coordinates. The software then generates a drawing of the initial positions for user inspection and error checking (Fig. 4).

The model can be used to perform a wide range of linkage simulations and calculations of force vectors and magnitudes. As described below, the pharyngeal four-bar linkage is composed of three skeletal elements and a muscle. A posterior portion of the skull is the fixed link, the levator posterior (LP) muscle is the input link, and epibranchial 4 (EB4) and pharyngobranchial 3 (PB3) are the movable coupler and output links, respectively. Four-bar linkage simulations with a muscle as part of the design have been performed previously with the sternohyoideus muscle of the hyoid linkage (Westneat, 1990). The implications of this are that the linkage may only operate with the muscle link in tension (not compression). Due to its key position as a primary element of the linkage, we used LP contraction as the primary input that

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determines the motion of the linkage and the positions of all movable points, including the attachment points of other muscles in the system. The lengths of the other three muscles in the system were either held isometric (OP) or were contracted to a length that corresponded to the new positions of their attachment points following LP shortening (LE, OD). The model allows independent contractions of all 4 muscles, but for the present study we forced the LE, OD and OP to behave in coordination with the LP to limit the range of possible muscle contraction patterns that could be simulated. To simplify the simulations, we also assumed that the skull (fixed link) and the lower pharyngeal jaw were being held in fixed positions, though both these skeletal elements are capable of motion in living fishes.

The first question we addressed with the model is: what are the linkage kinematics of the upper pharyngeal jaw given a 10% contraction of the LP muscle? We simulated a dynamic contraction of the LP muscle in increments of 0.5% resting length up to 10% shortening. This simulation focuses on linkage motion, and assumes that the linkage is free to move and that the upper jaw closes toward the lower jaw without encountering a prey item. The simulation steps and variables calculated were the following:

1. LP shortening: contraction in increments of 0.5% until 10% total shortening achieved.
2. LP rotation angle: shortening of the LP causes the LP link to swing medially as EB4 rotates (Fig. 5).
3. EB4 rotation angle: shortening of the LP and maintenance of an isometric OP causes rotation around the fulcrum of the EB4 lever (Fig. 5).
4. PB3 rotation angle: EB4 rotation causes ventral motion of the lateral margin of PB3, rotating it toward the lower pharyngeal jaw into bite position (Fig. 5).

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5. Kinematic transmission coefficients: output rotation of the PB3 is used as numerator in KT ratios with denominators of LP rotation (KT PB3/LP) and EB4 rotation (KT PB3/EB4).
6. Gape: distance between toothplate of PB3 and lower pharyngeal jaw.
7. Bite vector distance- distance traveled by PB3 toothplate.
8. Bite vector angle- angle of travel of PB3 toothplate relative to Y-axis (straight down).
9. LE contraction: contraction distance and percent of LE.
10. OD contraction: contraction distance and percent of OD.
11. Linkage angles: key angular relations such as that between LP and EB4 and EB4 and PB3.

The second question we asked through use of the computer model was: how do the pharyngeal muscles transmit muscle forces through the pharyngeal linkage? We examined each of the positions of the closing pharyngeal jaws for its potential to exert bite force on a prey item, if a prey item were encountered between the jaws at that position. Each of the four muscles included in the model attach to the epibranchial and exert force on the linkage system in two complementary ways. First, each muscle has a force vector that causes rotation of the epibranchial as a lever, with different insertion angles and inlever and outlever distances. Second, each muscle produces a force vector that causes a medial translation of the epibranchial toward the pharyngobranchial, mediated by the geometry and kinetics of the four-bar linkage. We arbitrarily set the contraction force of each muscle at 1.0N and computed the fraction of that force that was effectively transmitted through the epibranchial lever and the pharyngeal linkage to the pharyngobranchial as bite force. These computations, performed dynamically at each iteration of the model, through the 10% LP contraction, involved resolving the force balance of each muscle at each joint, and calculating mechanical advantage, torque, linkage force transmission, and final bite force. The variables calculated were the following:

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1. Mechanical advantage (MA): the ratio of inlever to outlever for each of the four muscles was computed. MAs remain constant throughout the pharyngeal bite.
2. Effective mechanical advantage (EMA): mechanical advantage multiplied by the sin of the angle of muscle insertion. EMAs change dynamically as linkage rotation occurs.
3. Lever torque: output force of the lever multiplied by moment arm of EB4.
4. Lever bite force: resultant lever force vectors onto the PB3 toothplate in the direction of gape closing from each muscle.
5. Linkage bite force: resultant linkage force vectors onto the PB3 toothplate in the direction of gape closing from each muscle.

Results:

Anatomy of the pharyngeal four-bar linkage

The biomechanical configuration of the musculoskeletal elements of the upper pharyngeal jaws of *Sciaenops ocellatus* resembles that of an obliquely oriented, planar four-bar linkage that is discussed in detail below (Fig. 3B). The key skeletal element of the upper jaw model is the elbow-shaped 4th epibranchial bone (EB4) that articulates through a synovial hinge joint with the 3rd pharyngobranchial toothplate (PB3) (Fig. 2B). The longer medial arm of EB4 connects cartilaginously at this joint with the posterior lateral margin of PB3 and abuts the adjacent dorsal surface of PB4. The EB4 directly connects the upper jaws to the lower jaw elements through a flexible u-shaped cartilage to the 4th ceratobranchial (CB4) at its shorter distal arm (Fig. 2). The 3rd epibranchial bone (EB3) also articulates with the lateral margin of PB3 through a similar synovial joint just anterior to EB4. In addition, EB3 also has a large posterior extending uncinat process that overlaps and connects via a robust ligament to the bend

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of EB4 on its mid-dorsal surface (Fig. 2A). This tight connection between epibranchial bones causes any motion in EB4 resulting from muscular input to be transmitted in a similar fashion to EB3 and vice versa.

The 3rd and 4th pharyngobranchial toothplates are loosely attached via ligaments along their adjacent margins making them semi-independently mobile. The PB3 toothplate's large size and predominance of large conical teeth identify it as the main biting element in the upper pharyngeal jaw (Fig. 2B). Its medial edge is invested in a cartilaginous pad that connects to its bilateral homologue and cushions this bone against the ventral portion of the parasphenoid bone of the endocranium. The anterior tip of PB3 wedges itself against a smaller 2nd pharyngobranchial toothplate restricting independent anterior movement. The anterior lateral anterior margin of PB3 also articulates through a flexible cartilage joint to the medial end of an elongate 2nd epibranchial bone (not shown).

Upper jaw biting motions are primarily driven by contractile activity in four main pharyngeal muscles: levator posterior (LP), levator externus 3/4 (LE), obliquus dorsalis 3 (OD), and obliquus posterior (OP) (Table 5; Fig. 3A). Coordinated contractions in these muscles adduct the pharyngeal jaws by ventrally depressing the lateral margins of the enlarged 3rd pharyngobranchial toothplates. The LP and LE are relatively long parallel fibered fusiform muscles that originate in the exoccipital and prootic region of the endocranium, respectively, and insert onto the dorsal face of the distal arm of EB4 traversing the elbow bend of EB4 where the uncinat process of EB3 attaches (Fig. 3). The angle of insertion of the LP onto the EB4 is greater than LE resulting in a more dorsal line of action compared to the more anteriorly oriented LE (Fig 3). The OD is the biggest muscle with a short overall length and large cross-sectional area that originates on a medial process on the dorsal surface of the PB3 and has a broad area of

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attachment onto the medial arms of EB4 and EB3, as well as the large overlapping uncinuate process of EB3 (Table 1; Fig. 3). Finally, the OP originates from the concave ventral surface of the EB4 elbow and attaches to the medial posterior process of the lower toothplate, CB5 (Fig. 3).

Computer modeling of pharyngeal jaw kinetics

Coordinate morphometric data (Table 3) were analyzed using the biomechanical linkage model PharyngoModel 2.0. The four main muscles that attach to the linkage system transmit force and motion to the pharyngeal apparatus by rotating the epibranchial and pharyngobranchial. Muscle shortening of the LP and the OP was defined by the model simulation (10% and 0% respectively), whereas shortening of the LE and OD was determined by linkage position (Table 4). LE contraction was similar to LP in contraction percentage, usually with a greater contraction distance and OD contraction percentage was higher than the other muscles, ranging from 15-20% (Table 4). The force vectors for each muscle can be separated into a component of force transmission due to lever mechanical advantage, and a component due to linkage transmission (Fig. 5). The LP and LE muscles both insert on the distal arm of EB4, so that contraction of these muscles causes EB4 to behave as a first class lever mechanism nested within the upper jaw 4-bar linkage (Fig. 2B, Fig. 5A). The elbow of EB4 acts as the fulcrum (point of rotation) and is the site of attachment of the OP muscle, which resists dorsal movement (Fig. 3B, Fig. 5A). Shortening of the LP or LE at their insertion on the distal arm of EB4 generates a medio-ventral torque at the fulcrum that transmits muscular force down EB4's medial arm (output lever) to its synovial hinge joint with the upper toothplate (PB3). A component of this force causes the pharyngobranchial to rotate ventrally in its biting motion. The simple mechanical advantage of LP ranged from about 0.6 to 0.8, and that of the LE was

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generally about half that of the LP, reflecting its insertion between LP attachment and lever fulcrum. Effective mechanical advantages (EMA), however, were considerably lower due to the acute angle of insertion of both muscles onto the EB4 inlever (Table 4). EMA is dynamic, changing with changing insertion angle, and it is notable that both LP and LE show increasing EMA from beginning to end of the bite cycle.

The action of the OP and OD muscles were analyzed with a similar force vector analysis (Fig. 5B, C). The OP muscle, contracting isometrically under our simulations, provides a steady fulcrum for the EB4 link but also may contribute to bite force when a prey item is between the jaws (Fig. 5B). Acting as a 3rd class lever, the vector V1 of the OP is perpendicular to the inlever, imparting force to the EB4/PB3 joint that is transmitted to the prey as bite force. The action of OD is more complex because both origin (PB3) and insertion (EB4) are on mobile, rotational elements. Thus, OD contraction has an effective force vector (Fm) that may draw the origin and insertion together (Fig. 5C). The primary lever action of OD is to rotate PB3 dorsally (V1 is directed the wrong way for bite force) but the angle of insertion (angle α) is highly oblique, almost 180° in most simulations, so that this force component is negligible. OD has a powerful linkage action, as it swings EB4 toward PB3 with a vector determined by angle β (Fig. 5C), providing a large percentage of total OD force as effective bite force.

The mechanical advantages of the OP and OD were similar, ranging from about 0.5 to 0.8, but EMAs were strikingly different (Table 4). OP has the highest EMA of the 4 muscles due to its nearly 90° angle of insertion onto its inlever which increases its force potential as the linkage closes during a bite. The OP reaches an EMA of 0.6-0.7 as the jaws are closed. In contrast, the lever EMA of the OD is the lowest of the 4 muscles, with the negative EMA values showing that the muscle actually tends to pull the pharyngobranchial upwards, in the opposite

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direction of the bite force (Table 4). However, as detailed below it should be noted that muscles with a weak lever advantage tend to have a high proportion of their force used in rotating the linkage medially, contributing in that way to bite force.

Under conditions of no load or resistance due to a prey item being bitten, the simulated kinematics of the pharyngeal mechanism (Table 4, Figs. 6, 7) reveal that the vector of upper jaw toothplate (PB3) motion results in a gape change of 0.2- 0.3 cm over the simulated muscle contraction (Fig. 6A). The total distance traveled by the PB3 toothplate is slightly greater than that, because the toothplate travels on a vector angle that ranges between 10 and 20 degrees medioventrally (Fig. 6 B, C). The rotation of the EB4 element is approximately twice PB3 rotation during an unloaded bite simulation (Fig. 7A, B), with EB4 rotation approaching 20°. This results in a kinematic transmission ratio for the pharyngeal linkage of nearly 0.5 (Fig. 7C) during the closing cycle.

We used the linkage model to perform a force vector analysis for each stage of jaw closing to calculate the bite forces if a prey item were in the position to be bitten between the pharyngeal jaws at each linkage position. Results show that forces for the pharyngeal bite are transmitted primarily by swinging the linkage medioventrally, rather than by lever mechanics of the EB4 or PB3 (Fig. 8). The total summed input force for all muscles was 4.0N, of which more than half (2.3-2.6N) was transmitted as bite force output (Fig. 8C). Most of that total bite force is due to linkage transmission (Table 5; Fig. 8B) whereas only a small fraction of that (0.1-0.4 N) was delivered by lever mechanics (Fig. 8A). However, analyzing the bite force components of each individual muscle (Table 5; Fig. 9) reveals that the four muscles make their contribution to bite force in somewhat different ways. The OP muscle has a high lever torque (Fig. 9A) and lever output (Fig. 9B) due to high EMA, but a relatively low contribution to linkage force

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transmission (Fig. 9C). Interestingly, however, the OP linkage force increases steadily during jaw closing. In contrast, the OD muscle had low lever torque and force, but consistently high linkage transmission (Fig. 9). The LP and LE muscles were intermediate in lever force transmission and were lower than the other two muscles in their linkage transmission toward the end of the bite cycle.

Discussion

The mechanism of upper jaw depression in the pharyngeal arches of *Sciaenops ocellatus* can be modeled as a four-bar linkage. Like the hyoid linkage, our four-bar model employs a shortening muscle (LP) as the primary effector of motion in the system. The hypothetical bite kinetics of *S. ocellatus* depicted by the model help to explain how the upper toothplate, PB3, with its large canine-like teeth moves and transmits force to puncture and grasp prey items. We found that the major muscles of the pharyngeal jaws had poor effective mechanical advantage and most produced low torque and output force from lever transmission alone. We conclude that the four-bar linkage arrangement is critical to the development of pharyngeal bite force, which was approximately 65% of the total input force of the main pharyngeal muscles. The modeled upper jaw biting motions in *S. ocellatus* are functionally critical for prey processing in that they break down the structural integrity of the prey and facilitate transporting it to the esophagus. The development of the computer model (PharyngoModel 2.0) that generates dynamic simulations of upper pharyngeal jaw kinetics from anatomical digital photos gives us a powerful predictive tool providing testable hypotheses of pharyngeal bite performance in generalized perciform fishes.

PharyngoModel Simulations of Pharyngeal Jaw Mechanics

Biomechanical models of feeding systems in vertebrates offer insight into the basic process of force and motion transfer during important behaviors, allow analysis of developmental trajectories of functional design, and promote comparative and phylogenetic analyses of key functional traits (Westneat, 1995; Westneat et al., 2005). Here we propose a biomechanical linkage model as a first step forward in our ability to interpret function from structure in the complex design of pharyngeal jaws. The morphological basis of biting in the pharyngeal jaws was most clearly illustrated by Wainwright (1989) who developed a model that identified an upper jaw depression mechanism as the primary working stroke of jaw occlusion. He discovered a previously unrecognized force coupling of the epibranchial-pharyngobranchial joint whereby independent activity in the levator posterior, levator externus, and obliquus doralis rotated the fourth epibranchial arch about a fulcrum defined by the ventral insertion of the adductor branchialis and obliquus posterior. Wainwright's (1989) proposed mechanism describes this anatomical coupling as a first class lever that transmits contraction force from the upper jaw muscles through the joint resulting in ventral depression of the lateral margin of the upper toothplate.

The linkage proposed here incorporates Wainwright's proposed lever mechanism and uses it as a central part of the mechanism by which linkage rotation and bite force are produced. The added value of developing a linkage model is that additional muscles can be incorporated into the mechanism, and dynamic, iterative calculations of force vectors can be made at each stage of the pharyngeal bite. For example, we used the model to decompose the forces exerted by each muscle into orthogonal vectors that are transmitted by lever torque and those transmitted by rotational action of the entire four-bar linkage (Table 5, Fig. 9). We found that linkage

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transmission was considerably more forceful than lever transmission, but that both were required to understand the complete force balance of the pharyngeal bite (Fig. 8). Indeed, we found that muscles such as the OP and the OD differ considerably in the relative importance of lever and linkage transmission (Table 5; Fig. 9), and we conclude that the considerable muscle subdivision or duplication in the pharyngeal apparatus may be due, in part, to the functional advantages of using alternative force transmission strategies among the muscular motors driving the system.

One critical finding of Wainwright's lever model showed that upper jaw depression does not work without the key mechanical linkage that the obliquus posterior provides in resisting dorsal elevation of the epibranchial arch (Wainwright, 1989). In congruence with Wainwright's findings, our simulations explicitly quantify how a resistive isometric contraction of obliquus posterior (OP) inserting onto the 4th epibranchial bone is functionally critical in transmitting high lever forces and torque through the arch as well as dynamically increasing its linkage force contribution during the bite (Figs. 5B & 9). It is important to note that what prevents the OP from lifting the lower jaw (CB5) dorsally, and thereby allows it to be modeled as a resistive element in the linkage, are observations in *S. ocellatus* that show the pharyngocleithralis muscles are simultaneously active with the OP during prey processing and are anatomically oriented to stabilize and depress the lower jaw against the cleithrum of the pectoral girdle (Grubich, 2000).

Pharyngeal Jaw Biomechanics in S. ocellatus

PharyngoModel simulations generate predictions of pharyngeal strength in *S. ocellatus* under the assumption that all pharyngeal muscles contract simultaneously after the onset of linkage motion input from the levator posterior. In fact, the model is unusual in that linkage transmission only works when the LP is contracting. We are confident that this inherent

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assumption of the model is biologically realistic in *S. ocellatus*. During manipulations of the specimens, placing objects between the upper and lower jaws (as a prey item might be) had the effect of rotating the 4th epibranchial postero-laterally which placed the levator muscles in tension. In addition, motor patterns of *S. ocellatus* show simultaneous onset and overlapping durations of upper jaw muscles during crushing of hard crabs and raking transport of soft shrimp prey (Grubich, 2000). Indeed, this aspect of the model may make it broadly applicable since simultaneous EMG activity in upper pharyngeal muscles during pharyngeal transport behavior appears to be a conserved motor pattern trait in generalized perciform fishes (Wainwright, in press).

Recent sonomicrometry and cineradiography research of pharyngeal jaw motions during prey processing also lend strong support to our predictions of bite kinetics in *S. ocellatus*. Direct measurements of upper toothplate ventral depression during pharyngeal transport in *Diplodus sargus* (Sparidae) (Vandewalle et al., 1995) and *Micropterus salmoides* (Centrarchidae) (Wainwright, in press) shows a bite excursion of 0.2- 0.3 cm, which is the same range in gape change predicted for *S. ocellatus* by our model (Table 4, Fig. 6). Furthermore, with the assumption of a fixed antero-medial edge of PB3 built into the model, bite vector angle and distance demonstrates a medially swinging trajectory of the upper toothplate in *S. ocellatus* (Table 4, Fig. 6). Sonomicrometry of the posterior view of the upper jaw mechanism in *Scorpaenichthys ornatus* (Cottidae) supports this prediction by revealing that the lateral margin of PB3 in this species does indeed swing medially while the medial edge of the toothplate remains relatively motionless (Wainwright, in press). This bite motion also makes sense in the light of dentition patterns found in *S. ocellatus*. The largest conical teeth on the 3rd pharyngobranchial are position along the lateral margin of the toothplate directly underneath the

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joint with EB4 where the largest force and greatest bite excursion are transmitted by the linkage to the prey (Fig. 2B).

Linkages in Fish Feeding Systems

Four-bar linkage models accurately quantify cranial kinesis in the oral jaws and hyoid apparatus involved in jaw protrusion and suction generation in some fishes (Anker, 1974; Aerts and Verraes, 1984; Muller, 1987b; Westneat, 1990; Westneat, 1994). While these models describe the underlying biomechanics involved in prey capture, our model, in contrast, delves into the previously unexplored feeding behaviors involved in prey processing by an unusual linkage in the pharyngeal jaws. A common metric used to describe the transmission of force and motion through four-bar linkages is the kinematic transmission coefficient (KT) (Barel, 1977; Westneat, 1994). Because this dimensionless ratio is size-independent, it has been repeatedly used for comparing morphological diversity in linkage mechanics among the speciose labrid fishes (Alfaro et al., 2004; Hulsey and Wainwright, 2002; Westneat, 1994, 1995; Westneat et al., 2005). Kinematic transmission ratios can be thought of as a measure of the output velocity of a linkage with its inverse being proportional to its force output. In labrid feeding mechanics, KT's for hyoid linkages range from 2.0 to > 3.0 emphasizing the need for speed in hyoid depression to generate sufficient suction for prey capture (Westneat, 1994). In comparison, our simulation of pharyngeal jaw kinetics resulted in the lowest KT's yet estimated in fishes (i.e. PharyngoModel mean $KT < 0.5$, $n = 6$; Table 4, Fig. 7) indicating the pharyngeal jaws linkage in *S. ocellatus* is modified for transmitting strong forces that are needed for biting and crushing during the slower masticatory behaviors of prey processing.

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Future modeling will seek to develop a 3-dimensional model that can account for the anterior/posterior shearing jaw motions common in perciform pharyngeal jaws (Grubich 2000; Wainwright, in press). A key component of such a model will integrate force input from the retractor dorsalis and levator interni muscles that antagonistically pull the upper jaws along the anterior/posterior axis. The model will also need to resolve the transfer of muscle forces through the repeated skeletal arrangement of the upper branchial arches that appears to be a series of interconnected linkages and levers (Fig. 2 A). For example, how does the bony connecting strut of the 3rd epibranchial bone affect the spreading of bite forces anteriorly and medially across the upper toothplate? Furthermore, more complex models will need to incorporate bite forces and kinetics of the other upper toothplates (2nd and 4th pharyngobranchials), possible lateral motion of the upper jaws, and the motions of lower jaw (CB5), to build a more complete understanding of pharyngeal jaw biomechanics in generalized perciform fishes. However, we suggest that the present model provides specific predictions regarding jaw motion and force capability that might readily be tested using sonomicrometry and strain gauge technology in bite force experiments.

Pharyngeal Jaw Modeling: Comparative Functional Diversity and Ecomorphology

The pharyngeal jaws are an important component of most teleostean feeding mechanisms and have played a key role in the evolution of fish feeding (Grubich, 2003; Lauder, 1983b; Lauder, 1992; Wainwright et al., 2004). Thus, our understanding of the mechanics of the pharyngeal bite will aid in the explanations of feeding ecology and functional diversity in fishes. For example, functional decoupling of prey capture and processing mechanisms between the oral and pharyngeal jaws has been hypothesized as the driving force behind ecomorphological diversification (Lauder and Liem, 1989; Liem, 1978). With the advent of the four-bar linkage in

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PharyngoModel, we now have a tool to survey pharyngeal jaw KT's within an ecomorphologically diverse group of fishes. By comparing oral and pharyngeal linkage KT's, we will actually test the functional decoupling hypothesis by determining the extent of overlap between the mechanical properties of these functional systems. One expectation of functional decoupling predicts that species that feed on more variable diets (i.e. slow hard prey *and* soft evasive prey) will exhibit a greater difference in KT's between the oral and pharyngeal jaws reflecting each feeding systems specialization on prey capture (fast prey; high KT) and prey processing (durable prey; low KT), respectively.

The large amount of linkage force transmission that contributes to overall bite force was an unexpected outcome of the model. Interestingly, the mechanical arrangement of the obliquus dorsalis provides the dominant muscular input to linkage transmission (Fig. 9). The importance of the OD in generating bite force in *S. ocellatus* is morphologically reinforced by its large size relative to the other pharyngeal muscles (Table 1; Fig. 3). In relation to its diet, *S. ocellatus*, as mentioned earlier, feeds on a variety of prey from soft fish to hard-shelled crabs that require a strong pharyngeal bite to crack and puncture. In contrast, the closely related durophagous sciaenid, *Pogonias cromis*, which feeds on mollusks has an upper pharyngeal jaw architecture that includes extreme hypertrophication of the levator posterior muscle. A similar pattern is present in durophagous species of the Centrarchidae and Carangidae (Grubich, 2003; Lauder, 1983a; Wainwright, 1991) indicating lever force transmission may play a larger role for mollusk crushing in those taxa. To examine morphological diversity in pharyngeal muscles, users of the current model can simulate various force inputs among individual muscles (i.e., individually varying the default 1N input force) to determine the effects of muscle size on bite kinetics and force transmission of the linkage (Fig. 4).

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The four-bar linkage in the upper pharyngeal jaw mechanism produces a set of testable predictions of pharyngeal jaw bite force and kinematics. A key goal now will be to empirically test these results and determine how widespread the applicability of this model is among the diverse pharyngeal morphologies of the sciaenids and other generalized perciform fishes. Based on the morphological configuration of the pharyngeal apparatus and presence of raking, piercing or crushing teeth on the posterior arches, we predict that the model will be applicable to many perciform fishes, including some of the large marine families such as the Haemulidae (grunts), Lutjanidae (snappers), Sciaenidae (drums), Serranidae (groupers), Sparidae (porgies) and others. As currently constructed, this model would not be applicable to the muscular sling of the labroid pharyngeal jaw mechanism or to fishes that lack mobility of the pharyngobranchial to exert a bite onto the ceratobranchial lower jaw element. Future modeling efforts are focused on modifying the modeling software for other pharyngeal configurations and developing a more complex three-dimensional approach to the pharyngeal jaws. We suggest that PharyngoModel and its future iterations may prove to be a valuable tool for exploring such issues as ontogenetic change in musculoskeletal design and investigating the evolution of the vast morphological diversity of pharyngeal jaw architecture in perciform fishes.

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Figure Legends.

Figure 1. Parasagittal dissection of the branchial arches of *S. ocellatus* illustrating the multiple bone elements and extensive branchial musculature controlling pharyngognathly set deep within the gill chamber. Abbreviations: Lp (levator posterior), Le (levator externus $\frac{3}{4}$), Od (obliquus dorsalis), Eb (epibranchial), Cb (ceratobranchial).

Figure 2. Skeletal elements of the pharyngeal jaws of *S. ocellatus*. Dorsal view of the pharyngeal jaws looking down from the neurocranium (A). Lateral right side view of the 4th branchial arch upper jaw elements with lower toothplate, CB5 (B). Abbreviations: Eb (epibranchial), Cb (ceratobranchial), Pb (pharyngobranchial), Li (inlever), Lo (outlever).

Figure 3. Upper pharyngeal jaw dissection showing close up lateral view of digital landmarks of anatomical elements used to generate model simulations (A). Overlay depicting the morphometry of digital landmarks making up the links of the proposed four-bar linkage in the upper jaw mechanism (B). Blue lines/shapes depict bone links. Circles depict joint articulations and rotation points. Purple lines depict muscular links and input. Abbreviations: Lp (levator posterior), Le (levator externus $\frac{3}{4}$), Od (obliquus dorsalis), Op (obliquus posterior), Eb (epibranchial), Cb (ceratobranchial), Pb (pharyngobranchial), Li3 (3rd levator internus), Pci (pharyngocleithralis internus), Pce (pharyngocleithralis externus), Nc (neurocranium).

Figure 4. PharyngoModel 2.0 application screen showing application control features, linkage morphometric data calculated from input coordinates, simulation results, and a drawing of the

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linkage positions under the current simulation parameters. Simulation results can be viewed onscreen for inspection and error checking, or extended results may be written to output files.

Figure 5. Vector diagrams of the lever and linkage mechanisms in the pharyngeal jaws of *Sciaenops ocellatus*, showing the force vectors of (A) the levator posterior (LP) muscle (levator externus has a similar mechanism), (B) the obliquus posterior (OP), and (C) the obliquus dorsalis 3 (OD). Initial muscle force (F_m) can be decomposed into vectors (V_1 , V_2) that are perpendicular to an inlever (L_i) or provide a moment that swings the four-bar linkage medially. Input forces create torque (T_q) around a lever fulcrum (f) determined by the magnitude of V_1 , the angle of muscle insertion (α), and the length of the outlever (L_o). Forces from both lever (F_{lev}) and linkage (F_{link}) are transmitted to the pharyngobranchial to exert bite force (F_{bite}).

Figure 6. Kinematics of the pharyngeal bite of *Sciaenops ocellatus* as a function of LP contraction up to 10% of resting length. (A) Gape distance between pharyngobranchial tooth plate and lower pharyngeal jaw. (B) Distance traveled by the pharyngeal tooth plate toward the prey item. (C) Vector angle of travel of the pharyngeal toothplate relative to the y-axis (straight down) with positive angles indicating mediad translation of the toothplate. Error bars are standard deviations of the mean of 6 individuals.

Figure 7. Kinematics of the pharyngeal bite of *Sciaenops ocellatus* as a function of LP contraction up to 10% of resting length. (A) Rotation of epibranchial 4 (EB4). (B) Rotation of pharyngobranchial 3 (PB3). (C) Kinematic transmission coefficient of the pharyngeal four-bar

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linkage, calculated as PB3 rotation divided by EB4 rotation. Error bars are standard deviations of the mean of 6 individuals.

Figure 8. Relative bite force potential of the pharyngeal apparatus simulated by the model, expressed as total force assuming a constant 1.0N input force from each muscle (4N total for the four muscles) during a 10% shortening of the LP. (A) Force potential of the pharyngeal levers. (B) Force potential of the pharyngeal four-bar linkage. (C) Total bite force potential. Error bars are standard deviations of the mean of 6 individuals.

Figure 9. Simulated torque and force profiles for each of the four major muscles of the pharyngeal apparatus, assuming a constant 1.0N input force from each muscle during a 10% shortening of the LP. (A) Torque exerted by each muscle for its primary lever fulcrum (Fig. 5). (B) Lever output force for each muscle. (C) Force output of the pharyngeal four-bar linkage. Error bars are standard deviations of the mean of 6 individuals.

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Table 1. Average muscle masses of the upper pharyngeal jaw linkage in *Sciaenops ocellatus* (n = 6 individuals)

Muscle	Avg. mass (g)	SE	% of Total Muscle Input
LP	0.44	0.07	10
LE	0.96	0.14	21
OD	2.14	0.32	47
OP	0.55	0.08	12

Table 2. Description of digital landmarks used to model *S. ocellatus* pharyngeal jaw mechanics

Landmark	Anatomical Position
1	Origin of LP on endocranium
2	Anterior tip of PB3 articulating with endocranium
3	Articulation of proximal end of EB4 with lateral edge of PB3
4	Insertion of LP onto dorsal posterior end of EB4
5	Fulcrum of EB4 where posterior process of EB3 overlaps
6	Insertion of OD onto dorso-medial surface of PB3
7	Tip of lateral most canine tooth of PB3
8	Origin of OP on lateral posterior process of CB5
9	Mid ventral position of lateral surface of CB5
10	Anterior tip of toothed surface of CB5
11	Insertion of LE onto dorsal posterior end of EB4
12	Origin of LE on endocranium

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Table 3. Coordinate data from the pharyngeal jaw mechanism of 6 specimens of red drum (*Sciaenops ocellatus*).

Pt#	Individual											
	X1	Y1	X2	Y2	X3	Y3	X4	Y4	X5	Y5	X6	Y6
1	4.35	6.09	4.33	5.13	3.31	4.35	3.92	4.66	4.90	4.98	4.49	4.82
2	6.02	3.51	5.68	2.56	5.04	2.73	5.62	2.59	6.74	2.84	5.98	2.53
3	3.78	3.32	3.52	2.49	3.41	2.61	3.75	2.52	4.88	2.85	4.03	2.59
4	2.39	4.52	1.94	3.45	2.12	3.02	2.51	3.37	3.50	3.59	2.56	3.46
5	3.24	4.55	2.80	3.53	2.78	3.39	3.33	3.53	4.32	3.86	3.48	3.63
6	4.82	3.71	4.74	2.78	4.10	2.91	4.70	2.83	5.81	3.04	5.14	2.78
7	4.09	2.59	3.64	1.94	3.48	2.09	3.94	1.93	5.01	2.20	4.25	1.92
8	2.35	2.85	1.93	1.98	2.44	1.85	2.55	2.02	3.56	2.22	2.56	2.01
9	3.22	1.80	2.59	0.63	3.52	0.92	3.40	0.70	4.42	0.99	3.31	0.65
10	5.36	2.13	4.45	0.73	4.55	1.53	4.67	1.15	6.02	1.31	4.86	1.05
11	2.87	4.53	2.45	3.50	2.46	3.17	3.02	3.41	3.96	3.72	3.02	3.48
12	6.14	6.33	6.06	5.26	4.81	4.67	5.47	4.78	6.49	5.35	6.33	4.85

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Table 4. Muscle contraction parameters, mechanical advantage properties, and kinematics results of pharyngeal linkage simulation using a 10% contraction of the levator posterior muscle.

	Fish	1	2	3	4	5	6
Muscle Inputs							
LP contraction		0.28	0.29	0.18	0.19	0.20	0.24
LP percent		0.1	0.1	0.1	0.1	0.1	0.1
OD contraction		0.31	0.42	0.21	0.28	0.27	0.31
OD percent		0.15	0.20	0.15	0.18	0.16	0.16
LE contraction		0.30	0.44	0.20	0.27	0.27	0.29
LE percent		0.08	0.11	0.07	0.09	0.09	0.08
OP contraction		0.00	0.00	0.00	0.00	0.00	0.00
Muscle Advantage							
LP MA		0.63	0.68	0.75	0.76	0.75	0.80
LP EMA initial		0.29	0.41	0.31	0.46	0.40	0.40
LP EMA end		0.39	0.54	0.43	0.58	0.53	0.53
LE MA		0.32	0.34	0.38	0.38	0.38	0.40
LE EMA initial		0.06	0.12	0.02	0.11	0.09	0.07
LE EMA end		0.11	0.20	0.08	0.18	0.17	0.15
OP MA		0.63	0.68	0.75	0.76	0.75	0.80
OP EMA initial		0.52	0.56	0.56	0.59	0.54	0.61
OP EMA end		0.58	0.64	0.64	0.68	0.64	0.70
OD MA		0.54	0.45	0.59	0.51	0.51	0.45
OD EMA initial		-0.06	-0.06	-0.09	-0.11	-0.15	-0.08
OD EMA end		-0.18	-0.17	-0.22	-0.20	-0.26	-0.17
Kinematics							
Gape Initial		0.37	0.72	0.39	0.45	0.48	0.57
Gape Closed		0.13	0.43	0.22	0.29	0.30	0.37
Gape Change		0.24	0.30	0.17	0.16	0.19	0.19
Bite Vector Distance		0.30	0.46	0.21	0.23	0.26	0.28
Bite Vector Angle		14.6	18.7	14.0	20.2	11.2	22.9
EB4 rotation		17.4	22.6	15.7	18.2	18.4	17.6
PB3 rotation		8.0	12.3	7.0	7.3	8.2	8.8
KT		0.46	0.54	0.45	0.40	0.45	0.50

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Table 5. Total bite force, lever/linkage bite force components, torque, and individual force profiles for 4 pharyngeal muscles across 6 individuals of *Sciaenops ocellatus*.

Fishnum	1	2	3	4	5	6
ForceIn	4	4	4	4	4	4
BFLev	0.13	-0.08	0.05	-0.20	-0.09	-0.02
BFLink	2.49	2.32	2.47	2.28	2.39	2.42
BFTotal	2.62	2.25	2.52	2.08	2.30	2.40
Tq LP1	0.46	0.61	0.42	0.61	0.53	0.51
Tq LP2	0.62	0.80	0.57	0.76	0.70	0.67
Tq LE1	0.18	0.35	0.04	0.27	0.24	0.18
Tq LE2	0.36	0.58	0.21	0.47	0.44	0.38
Tq OD1	0.11	0.14	0.15	0.21	0.29	0.19
Tq OD2	0.34	0.38	0.37	0.40	0.50	0.39
Tq OP1	0.83	0.83	0.74	0.78	0.73	0.76
Tq OP2	0.92	0.95	0.85	0.89	0.86	0.88
BFLevLP1	0.19	0.23	0.18	0.16	0.20	0.20
BFLevLP2	0.11	0.04	0.10	0.00	0.06	0.06
BFLevLE1	0.04	0.07	0.01	0.04	0.04	0.04
BFLevLE2	0.03	0.01	0.02	0.00	0.02	0.02
BFLevOD1	-0.06	-0.06	-0.09	-0.11	-0.15	-0.08
BFLevOD2	-0.18	-0.17	-0.22	-0.20	-0.26	-0.17
BFLevOP1	0.34	0.31	0.32	0.21	0.27	0.30
BFLevOP2	0.17	0.04	0.15	0.00	0.08	0.08
BFLinkLP1	0.47	0.50	0.44	0.44	0.43	0.48
BFLinkLP2	0.49	0.43	0.45	0.36	0.40	0.46
BFLinkLE1	0.52	0.58	0.48	0.54	0.50	0.55
BFLinkLE2	0.58	0.58	0.53	0.48	0.50	0.58
BFLinkOD1	0.67	0.70	0.70	0.71	0.74	0.71
BFLinkOD2	0.74	0.66	0.76	0.65	0.75	0.69
BFLinkOP1	0.43	0.37	0.51	0.61	0.52	0.47
BFLinkOP2	0.67	0.66	0.73	0.79	0.75	0.70